

Food System of Tephritid Fruit Flies in Hawaii¹

T. NISHIDA¹

COLLEGE OF TROPICAL AGRICULTURE
UNIVERSITY OF HAWAII,
HONOLULU, HAWAII

Fruit flies, family Tephritidae, are among the most serious pests of fruits and vegetables in the temperate, subtropical and tropical areas of the world. Among insects of economic importance they are without doubt one of the important groups in the agro- and non-agroecosystems. It is indeed unfortunate that during the past seventy-nine years three species became established in Hawaii: the melon fly, *Dacus cucurbitae* Coquillett, in 1898 (Clark, 1898) the Mediterranean fruit fly *Ceratitidis capitata*, (Wiedemann), in 1910 (Back and Pemberton, 1918); and the oriental fruit fly, *Dacus dorsalis* Hendel, in 1946 (Van Zwaluwenburg, 1947). Because of their economic importance research has been in progress in Hawaii at various levels of intensity ever since the first species, *D. cucurbitae*, was found. These studies have contributed much towards our knowledge on fruit flies. However, there is much to be learned before we can develop effective management strategies against these pests.

Like many other insects, food is one of the important components of the environment that influences the abundance of fruit flies. The present contribution is in a sense a synthesis in which an attempt is made to put together food resource, food system, and population into an ecological system which might be useful in developing management strategies against these pests. Information on feeding habits and kinds of food under field conditions was obtained from various publications: Back and Pemberton, 1917, 1918; Nishida, 1953; Christenson and Foote, 1960; and Bateman, 1972. In addition, unpublished information from the author's field notes and data were used.

FOOD SYSTEM

In a food system it is necessary to give consideration to the behavior of fruit fly adults in regards to obtaining food. Evidences indicate that fruit fly adults are foragers. Like the large mammalian herbivores, they seem to move freely throughout the ecosystem in search of food. They tend to remain in localized areas, perhaps temporarily, where food is present and move into other areas when food becomes scarce. This type of behavior involves the dispersive and non-dispersive movements pointed out by Bateman (1972), who stated that these movements are related to food scarcity as well as to perturbation in the habitat. The foraging range of fruit flies may vary to some extent with the species. The Hawaiian species of fruit flies, are strong fliers capable of flying long distances. The long

¹ Published with the approval of the Director of the Hawaii Agricultural Experiment Station as Journal Series no. 2179.

² Acknowledgement. For their assistance in the field aspects of this work I wish to extend thanks to my former graduate students: Dr. Barton Matsumoto, Dr. Harry Kaya, and Dr. Mervyn Kamran. The author also acknowledges with thanks the constructive criticisms of Dr. Ernest Harris, Research Leader, Hawaiian Fruit Flies Laboratory.

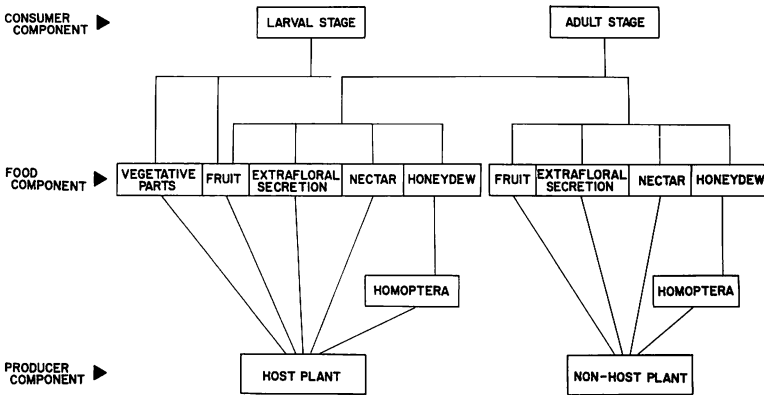


FIGURE 1. A model of the food system of the tephritid fruit flies in Hawaii.

range movements of *D. dorsalis* are well documented (Steiner et al., 1962; Iwahashi, 1972).

The food system of tephritid fruit flies in Hawaii is shown in figure 1. It consists of three basic components; producer, food, and consumer. The producer component consists of the autotrophs of the ecosystem, the host and non-host plants. The food component includes the dietary needs produced directly or indirectly by the producer. The consumer component generally includes other species in addition to fruit flies. The present study, however, is concerned only with the larval and adult stages of fruit flies.

The foundation of the food system is the primary producer, the host and non-host plants. The host plants are important for they produce vegetative parts and fruits upon which the larvae feed. They also provide adult food in the form of fruit juices, extrafloral exudations, and nectar. In addition they support homopterous insects that produce honeydew, figure 1. The non-host plants play a similar role. Although they do not provide larval food, they produce adult food such as fruit juices, extrafloral exudation, and nectar. They also support homopterous insects that produce honeydew, a source of carbohydrates and amino acids. (Gray, 1952; Ewart and Metcalf, 1956). The presence of carbohydrates in extrafloral exudation has been reported by Clark and Lukefahr (1956). The importance of carbohydrates and amino acids in the diet of fruit flies has been reported by various workers (Marlow, 1945; Hagen and Finney, 1950; Nishida, 1953; Christenson and Foote, 1960; Matsumoto and Nishida, 1962). From figure 1 it is evident that the basic food requirements are present in the Hawaiian ecosystem and that the food system of fruit flies in Hawaii shows a high degree of diversity.

CROP CONTENT

The food material in the crop of the adults is liquid with varying

amounts of minute particulate matter. It is contained in a membranous sac located in the abdomen and attached to the esophagous by a filamentous tube, figure 2. The crop can be easily dissected out by placing the insect dorsal side up and making a medial incision from the thorax to the abdomen with a fine pointed scalpel. The crop, which is in the abdominal cavity, can then be lifted up by clamping the duct with a fine tipped forceps.

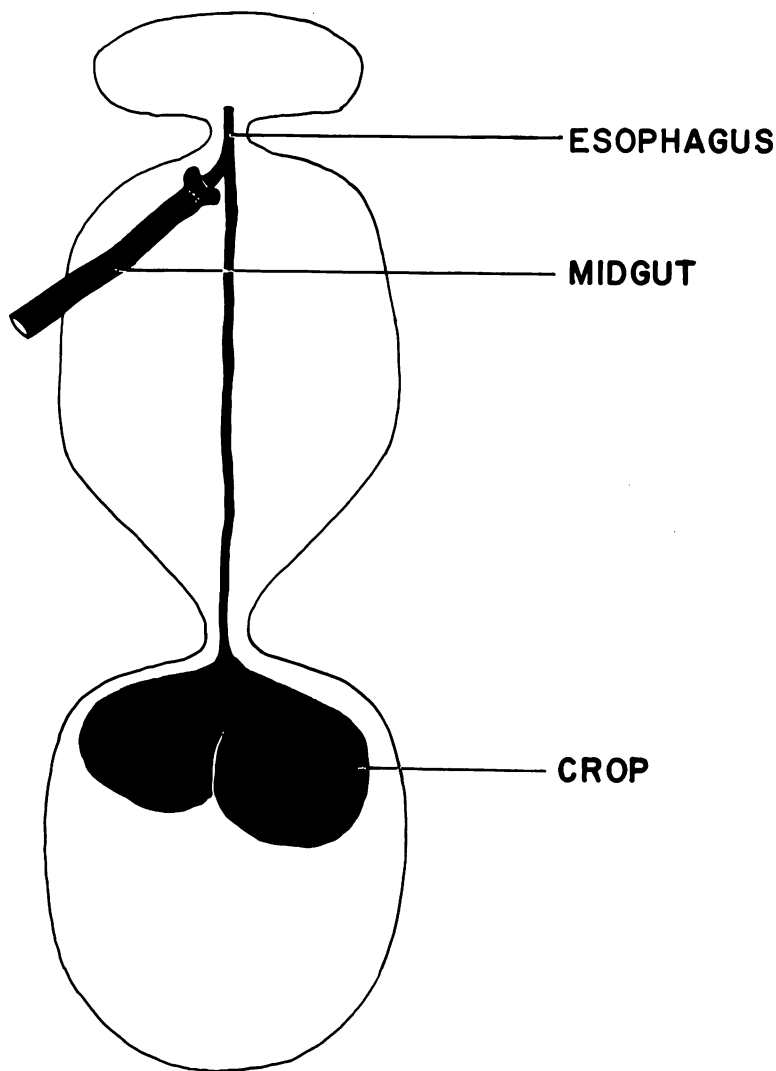


FIGURE 2. A crop dissected out of *D. dorsalis* showing the membranous sac, which contains the liquid ingested food, and the long duct which originates from the esophagus.

Studies on color and amount of food in the crop were conducted on *D. dorsalis*. The males were sampled from stands of wild guava, *Psidium guajava* L., using methyl eugenol as the attractant. A single drop of the attractant was placed on a conveniently located guava leaf. As soon as the flies landed on the leaf and before ingesting the methyl eugenol they were captured by use of an insect net. The flies were placed in 8-dram vials, which were immediately placed in a cooling box with ice in the bottom. The flies were then taken to the laboratory where they were killed in a cyanide killing jar. The crop of each fly was then dissected out under a microscope.

To determine the color of the food each dissected crop was lifted up with forceps and placed on a sheet of No. 2 Whatman filter paper. With a fine needle held vertically the crop was punctured approximately in the middle. The content of the crop soaked into the filter paper leaving an almost circular stain. On the white paper background the color of the stain remained visible for several months.

The volume of the liquid in the crop was estimated indirectly from the area of the stain on the filter paper. To do this it was necessary to know the relationship between volume of liquid producing the stain and area. This relationship was determined by use of micropipettes and sugar solution. The volume of liquid corresponding to the stained area was estimated by a calibration curve obtained by use of a series of micropipettes of known capacities in lambda units. The content of these pipettes, filled to capacity with a 20 per cent sucrose solution, was discharged on a No. 2 Whatman filter paper. The mean diameter of each stained area was then obtained using the maximum and minimum diameters. By regressing known volumes and corresponding areas calculated from the diameters, the relationship between volume and area was established. From this relationship the unknown volumes of the content of crops of field collected flies were estimated from the area of the stains of the filter paper.

Field samples of *D. dorsalis* were taken on Oahu during 1963 to 1966 from Helemano, Kaneohe, Waimanalo, and Tantalus. At each locality there was a sampling station where a total of 15 males were sampled from each at various intervals. The data presented in this paper are those taken only during 1964 and 1965 because they were taken regularly once a month at each locality.

Color as an indicator of food diversity

Data on the color of the crop content were taken from four areas of Oahu; Helemano, Kaneohe, Waimanalo, and Mt. Tantalus. As shown in table 1 a wide range of colors were found. They were brown, amber, clear, black, purple and yellow. In addition to these colors pink and gray were also observed in areas other than the study areas. The predominant color was amber; 85 per cent at Helemano; 73 per cent at Kaneohe; 72 per cent at Waimanalo and 84 per cent at Tantalus.

There were seasonal differences in the color of the crop content. For example, the clear color was noted at Tantalus and Kaneohe during June to December. Purple was observed at Waimanalo and Kaneohe during October to December.

Furthermore, it was found that certain colors tended to be specific to

TABLE 1. *Color variation in the crop content of D. dorsalis*. A total of 15 males were sampled from each locality at monthly intervals during 1965. Some totals do not add up to the sample because a few crops were deformed and empty.

Locality (Oahu)	Color	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Helemano	Brown	0	0	1	2	0	2	0	2	0	0	0	0
	Amber	10	15	10	13	13	10	15	13	15	11	15	10
	Clear	2	0	1	0	0	1	0	0	0	2	0	1
	Black	1	0	2	0	0	1	0	0	0	1	0	0
	Purple	2	0	0	0	0	0	0	0	0	0	0	0
	Yellow	0	0	0	0	0	0	0	0	0	0	0	4
Kaneohe	Brown	1	0	0	2	1	3	0	0	1	0	0	0
	Amber	13	12	12	12	13	12	12	10	11	4	11	11
	Clear	0	0	0	1	0	0	3	5	3	0	3	0
	Black	1	3	3	0	0	0	0	0	0	0	0	1
	Purple	0	0	0	0	0	0	0	0	0	10	1	3
	Yellow	0	0	0	0	0	0	0	0	0	0	0	0
Waimanalo	Brown	2	2	0	0	0	0	1	0	0	0	1	0
	Amber	11	13	14	12	15	14	12	11	11	7	7	0
	Clear	1	0	0	0	0	1	2	4	4	0	0	2
	Black	0	0	1	0	0	0	0	0	0	0	0	0
	Purple	1	0	0	0	0	0	0	0	0	8	7	13
	Yellow	0	0	0	0	0	0	0	0	0	0	0	0
Tantalus	Brown	0	0	0	1	0	0	0	0	0	0	1	0
	Amber	14	14	15	12	14	12	9	15	7	10	11	13
	Clear	0	0	0	0	0	1	4	0	6	4	3	2
	Black	0	0	0	0	0	0	1	0	0	0	0	0
	Purple	0	0	0	0	0	0	1	0	0	0	0	0
	Yellow	0	0	0	1	0	2	0	0	0	1	0	0

certain localities. Purple was not observed at Helemano, but was found at Kaneohe and Waimanalo, two adjacent areas. These color differences indicate variation in the kind of food, as well as locality specificity of certain foods.

Volume as an indicator of food quantity

The pooled data of the volume of the crops of flies sampled from Helemano, Kaneohe, Waimanalo, and Tantalus are shown in figure 3. The data were pooled because, with minor exceptions, there was no significant difference in crop volume of flies sampled from the four localities.

The data obtained indicate that the amount of food in the crop of wild flies deviated considerably from that of the well-fed laboratory flies which were fed water, sugar and yeast hydrolyrate. Out of a total of 96 mean values obtained during 1964 and 1965, 80 per cent of the samples fell below the level of the laboratory flies. These data indicate that the majority of the flies in the field were not ingesting adequate amounts of food. It might seem that the flies could be ingesting only water in some cases; however, laboratory tests showed that flies given only water do not engorge themselves as they do with favored foods.

Seasonal differences in the amount of food eaten seemed slight. Although there appeared to be a slight tendency for increase during July to

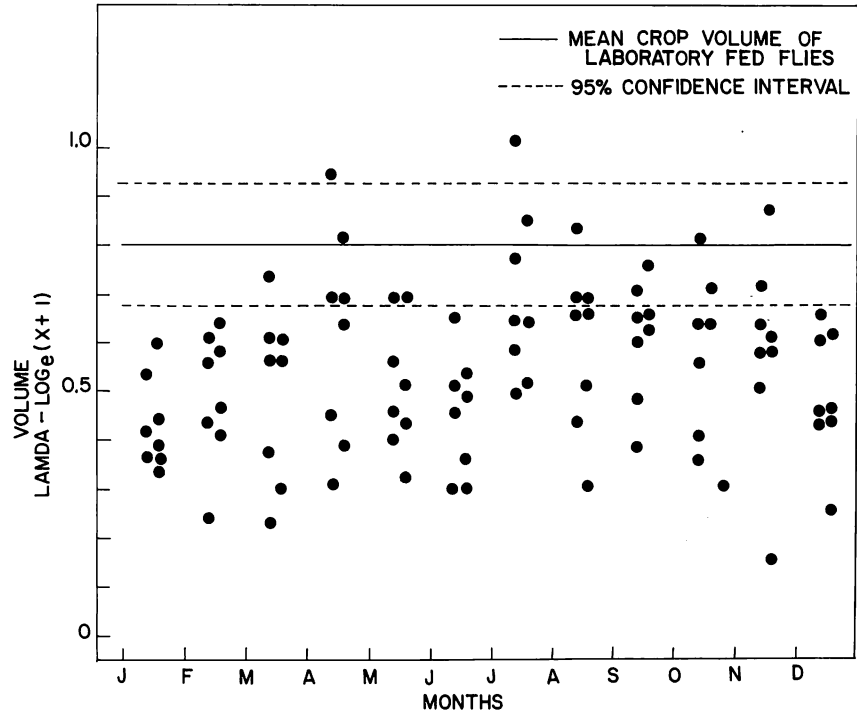


FIGURE 3. Crop content volume of field sampled flies in relation to laboratory-fed flies. Pooled field data of 1963-64 from Helemano, Kaneohe, Waimanalo, and Tantalus, Oahu were used.

October this trend was not distinct. This probably is an indication that rates of food consumption and renewal are in a state of equilibrium.

FOOD RESOURCE POPULATION MODEL

A model depicting the relationship between food resource and population is shown in figure 4. Food resources are shown as A and B; pool of adult population, C; and pool of reproductively active population, D. The developmental stages, adult, egg, larva and pupa are shown as E, F, G, and H, respectively.

The stages dependent upon the food resources of the ecosystem are the adult and larval stages. The pool of adults, C, contains reproductive and non-reproductive individuals which depend on food resource A. Dispersive and non-dispersive movements are involved in foraging. Individuals in pool D, which are those individuals in pool C that were able to obtain sufficient food for reproduction, produce offsprings in larval food resource, B. As in foraging, dispersive and non-dispersive movements are also involved here. The adults that emerge after passing through the egg,

larval, and pupal stages enter pool C, where they mingle and interact with the existing population.

Because all individuals depend on a common food resource there is no doubt of competition for food. Because the quantity of food is finite, a high population in the pool would result in some individuals not having adequate food, figure 3. The remaining 20 percent that do have adequate food enter pool D. Thus, there is an equilibrium between the rate of food renewal and food consumption. The magnitude of pool C depends therefore, on food resources A and B.

SOME PRACTICAL IMPLICATIONS

There are a number of implications that emerge from the material presented. It is not the intent of this paper to go into all of these. A few will be mentioned.

Field observations in the past have often shown an inconsistent correlation between adult fruit fly abundance and infestation by *D. dorsalis* and *D. cucurbitae*. In some areas the adult population may be high but the infestation is relatively low, while in others, the population may be sparse but the infestation is high. To a certain extent this situation may be due to age structure of the population; however, it may also be due to the abundance of underfed flies. Therefore, a high kill by insecticides may not necessarily result in a corresponding reduction in damage because the majority of flies killed could be non-reproductive underfed flies.

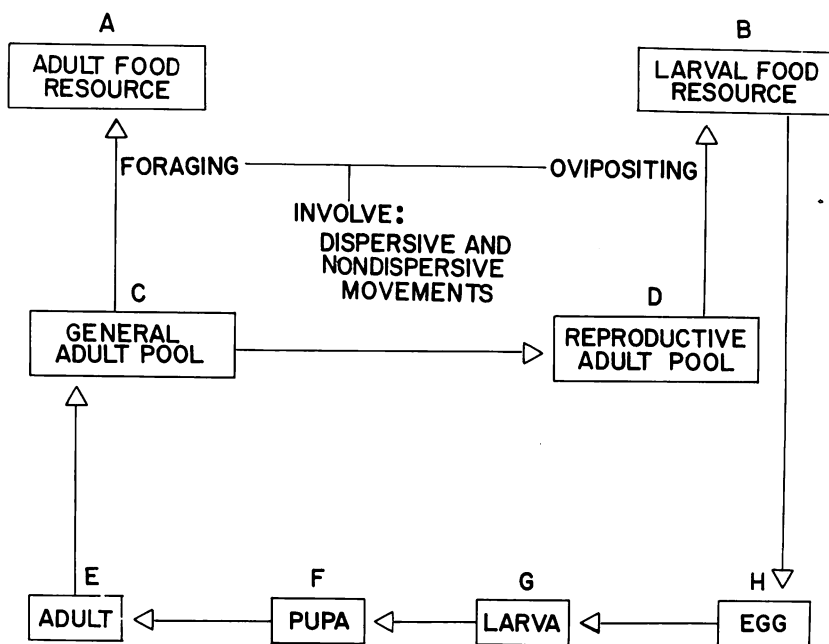


FIGURE 4. A model delineating the relationship between food resource and population of tephritid fruit flies in Hawaii.

Bait sprays have been used for the control of fruit flies. It has been noticed that many flies are often killed by baits, but the degree of control obtained was not in proportion to the kill. From the results presented in this paper, it seems that baits would kill first the under-fed flies because of their rapid response to food. Therefore, for effective control baiting must be carried out over a long time to reduce the number of adult flies in pool D, figure 4. Furthermore, baiting must be carried out continuously, otherwise the population will return to its original level within a short time.

The spraying of border plants for the control of the melon fly, *D. cucurbitae*, has been practiced. It was found that the fly population within a crop area can be more rapidly reduced by spraying certain border plants than by spraying the crop itself. The explanation for this becomes evident from figure 4 which shows that the rapid decline was due to the poisoning of the food resource A.

The sterile male release method for fruit fly population suppression may also be mentioned here. Theoretically, laboratory mass-reared sterile males released in the ecosystem will immediately enter the adult population pool C, figure 4. Because fruit flies can not live long without food and because the food resource A, is finite, mass releases of sterile flies will create a food stress in the ecosystem. Competition for food and mates among released and wild individuals is likely to occur, which could lead to the reduction in the size of the reproductively active population in pool D, figure 4, which is the desired objective. This objective may be the result of the combined effect of food and mating stresses imposed upon the population.

Competitive displacement among tephritid fruit flies in Hawaii has been a topic of discussion for a number of years. Let us examine the interaction caused by limited food resource from the model presented. Adults of different species would be in population pool D. Because they depend on a common food resource there would be competition for a limited food supply. It is possible that the outcome of such an interaction determines which species will dominate a given ecological area.

DISCUSSION

Fruit flies have a wide range of food resources in Hawaii. They are phytophagous as well as saprophagous. Micro-organisms, such as yeast, may be ingested together with decaying fruit juices. These may be important in providing nutrients; However, they are not considered in this paper. Likewise, although fecal matter has been reported to be eaten by adult flies, it was not discussed in this paper. Being an excreted material, it could be placed in the same category as honeydew.

The different colors of the crop content are indicators of different ingested material rather than changes that had occurred after ingestion. In the laboratory, where flies were fed sugar, yeast hydrolysate, and water, the only color noted were different shades of brown, the color of yeast hydrolysate. Since fruit fly adults commonly feed on fruit juices, the color of the crop content of wild flies may be due to the color of the juices ingested. The purple color noted in Kaneohe and Waimanalo during

October coincided with the fruiting season of the purple fruited plant, *Eugenia cumini* (L.) Druce. Likewise, the black color observed in the Helemano areas may be due to the feeding on the black-fruited popolo, *Solanum nigrum* L. These differences in the kind of food indicate that some of the foods are locality-specific. The richness of the food resource may also be area-specific. For this reason fruit flies must often "graze" over wide areas for food.

Crop volume measurements may be looked upon as a means of bio-assaying the ecosystem to determine the amount of food. However, the quality of food may be bio-assayed by fecundity for it is known that the quality of food influences fecundity (Marlowe, 1945; Hagen and Finney, 1950; Matsumoto and Nishida, 1962; Nishida, 1963). Fecundity data indicated inadequacy of food quantity and quality. The percentage of gravid *D. susurbitae* in the wild population during the year did not exceed 63 per cent (Nishida, 1963). Limited studies on *D. dorsalis* also indicated that it did not do any better. This conclusion differs from that of Pritchard in Australia who found that *Dacus tryoni* had ample food in an orchard (Pritchard, 1970). It should be mentioned that to obtain an over-all unbiased picture of gravidity in the ecosystem is difficult because gravid females and non-gravid females tend to be in areas with suitable shelter and food.

The present paper is an attempt to present a model of food system and population. It is not an ultimate one that delineates a true real life system in all respects. Further studies are needed. In the meantime, it might serve as a working model for practical work or a starting point for a more complete model.

ABSTRACT

Trephritid fruit flies, *Dacus cucurbitae* Coq., *D. dorsalis* Hendel, and *Ceratitis capitata* Wied., became established in Hawaii at various times during the past 79 years. One of the factors responsible for their success in Hawaii is food resource which provides them with sugars and amino acids, substances necessary for reproduction and longevity. These substances necessary for reproduction and longevity. These substances are produced directly and indirectly by the autotrophic component of the Hawaiian ecosystem. Practical implications on the control of these flies arising from the models presented are discussed.

LITERATURE CITED

- Back, E.A. and C.E. Pemberton. 1917. The melon fly in Hawaii. U.S. Dept. Agric. Bull. no. 491.
- Back, E.A. and C.E. Pemberton. 1918. The mediterranean fruit fly in Hawaii. U.S. Dept. Agric. Bull. no. 536.
- Bateman, M.A. 1972. Ecology of fruit flies. Ann. Rev. Entomol. 17:493-518.
- Christenson, L.D. and Richard Foote. 1960. Biology of fruit flies. Ann. Rev. Entomol. 5:111-192.
- Clark, B.O. 1898. Official bulletin of the Bureau of Agriculture. The Hawaiian. 1:6.
- Clark, E.W. and M.J. Lukefahr. 1956. A partial analysis of cotton extrafloral nectar and its approximation as nutritional medium for adult pink bollworms. Journ Econ. Entomol. 49:875-876.

- Ewart, W.H. and R.L. Metcalf. 1956. Preliminary studies of sugars, and amino acids in the honeydews of five species of coccids feeding in citrus in California. *Ann. Entomol. Soc. Amer.* 49:441-447.
- Gray, Reed A. 1952. Composition of honeydew excreted by pineapple mealy bugs. *Science* 115:129-133.
- Hagen, K.S. and G.L. finney. 1950. A food supplement for effectively increasing the fecundity of certain tephritid species. *Journ. Econ. Entomol.* 43(5):735.
- Hagen, K.S. 1956. Honeydew as an adult fruit fly diet affecting reproduction. *Proc. 10th Intern. Cong. Entomol.* 3:25-30.
- Iwahashi, O. 1972. Movement of the Oriental fruit fly adults among islets of the Ogasawara Islands. *Environ. Entomol.* 1(2):176-179.
- Marlow, Ralph H. 1945. Effect of foods on ovarian development in the melon fruit fly. *Journ. Econ. Entomol.* 38(3):339-340.
- Matsumoto, B. and T. Nishida. 1962. Food preference and ovarian development of the melon fly, *Dacus cucurbitae* Coquillett, as influenced by diet. *Proc. Hawaii. Entomol. Soc.* 18 (1):137-144.
- Nishida, T. 1953. Ecological study of the melon fly, *Dacus cucurbitae* Coq., in the Hawaiian Islands. Ph.D. thesis, University of California, Berkeley.
- Nishida, T. 1958. Extrafloral glandular secretions, a food source of certain insects. *Proc. Hawaii. Entomol. Soc.* 16 (3):379-386.
- Nishida, T. 1963. Zoogeographic and ecological studies of *Dacus cucurbitae* (Dipter-Tephritidae) in India. *Haw. Agric. Exp. Sta. Tech. Bull.* no. 54, University of Hawaii.
- Pritchard, G. 1970. The ecology of a natural population of Queensland fruit fly, *Dacus tryoni*. III The maturation of female flies in relation to temperature. *Aust. Journ. Zool.* 18:77-89.
- Steiner, L.F. and R.K.S. Lee. 1955. Large-area tests for a male annihilation method for oriental fruit fly control. *Journ. Econ. Entomol.* 48:311-317.
- Steiner, L.F., W.C. Mitchell, and A.H. Baumhover. 1962. Progress of fruit fly control by irradiation sterilization in Hawaii and the Mariana Islands. *Int. Journ. Appl. Radiat. Isotop.* 13:427-434.
- Van Zwaluwenburg, R.H. 1947. Notes and Exhibitions. *Proc. Hawaii. Entomol. Soc.* 13 (1):8.